THE CHANGE OF VEGETATION NEAR THE TIMBER-LINE

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ABSTRACT. — A timber-line in mountains may be considered as a spatial analog of the transition of the ecosystems through a critical state when the climate's bleakness increases. If the phytocenoses include dominant species — strong edificators, then the transition through critical state is sharp as in space as in time. The case is in accordance with the model "fold" of R. Tom's catastroph theory. In opposite case the transition is indistinct.

Key-words: USSR — The Caucasus — Siberia (Sayan Mountains) — Phytosociology — Altitude border of the forest.

RÉSUMÉ. — *La limite de croissance des arbres dans les régions montagneuses traduit le passage des écosystèmes à un état critique, en présence de conditions climatiques de plus en plus rigoureuses. Si les phytocénoses (associations végétales) comportent des espèces dominantes, la transition sera rapide dans l'espace et dans le temps, comme le laissait supposer le modèle dit « fold » de la théorie des catastrophes de R. Tom. En l'absence d'espèce dominante, par contre, la transition est indistincte.*

Mots clefs : URSS — Caucase — Sibérie (Mts Sayan) — Phytosociologie — Limite de la forêt avec l'altitude.

INTRODUCTION

The aim of this article is to consider the timber-line not from the usual descriptive positions, but as a spatial analog of the passing of an ecosystem through a critical state (a critical point). A critical state here is considered to be a transitional state of systems, in which their structure undergoes a qualitative transformation. Practically it means that the states of an ecosystem on one side from the critical point require for their description one model, on the other side — a different one. Ecosystems reach a critical state, as a rule, as a result of natural or anthropogenic changes of the environment surrounding the system or due to self-development. The critical state is unstable, as at this time the ecosystem is in discordance with its environment. The *transition process* brings the system from the critical state to one of the two alternative *homeostatic states*, in which equilibrium with the environment is restored.

Aggravation of the relations of mankind with the natural environment makes necessary a profound study of the *homeostatic properties* of ecosystems, conditions of their preservation and disturbance, conditions of the transfer of systems to the critical state and beyond it. However, systematic research on the critical states of ecosystems is often difficult because these states are transient while it takes too a long time to wait for their coming. In these cases quite useful may turn to be the method of spatial analogies, which in geography is better known as the *comparative-geographical method.* When studying critical states of ecosystems this method may help clear the question about inner mechanisms keeping systems in unfavourable conditions and about reasons for a rapid or a slow movement of systems to a new homeostatic state after passing the critical point.

THE COMPARATIVE-GEOGRAPHICAL METHOD

Alexander Humboldt (1845) is usually considered to be the "father" of the comparative-geographical method. One of the merits of this method lies in the fact that it makes it possible to replace changes of the system in time, which cannot be directly observed, by spatial series in which analogous systems at different stages of development are represented. Being situated in a row, in accordance with an increase of development features, these systems make it possible to form a notion about consecutive states of a system of the same type in the course of its evolution. This method was used by V. Davis (1954) while creating his theory of landscape (geomorphological) cycles, by V. Penk (1924) for studying evolution of slopes. Spatial rows are sucessfully used by phytocenologists and ecologists for studying the phenomenon of successions (Odum, 1971).

The comparative-geographical method cannot be substantiated with the same accuracy as the use of the ergodic principle in physics. It is due to the fact that choosing spatial series one can never completely fulfill the requirement : all the factors of the environment, influencing the state of the studied systems, should remain unchanged, except one —the *limiting factor* determining the course of development. However, the accuracy of our observations in nature is usually not so great for small deviations from this rule to give significant errors in the results.

When using the comparative-geographical method one should distinguish two instances. The first —when time is the limiting factor of the change of ecosystems, while in spatial series it is the age of systems. The second —when the change is conditioned both in time and in space by the change of one of the conditions of a system's existence : climate, hydrological regime, soils pollution, etc. In the first case we study the transition process or self-development, in the second —the process of a *forced development,* during which the system hardly deviates from a homeostatic state.

TIMBER-LINE AS AN ANALOG OF TRANSITION THROUGH A CRITICAL STATE

The profile crossing the natural border between forest and meadow landscapes, forest and tundra, forest and bog ones, etc. — may be considered as a spatial analog of the transition of corresponding ecosystems through a critical state. Naturally, if in such case the above formulated condition is not greatly upset. Depending on the fact from which side we cross the border, we may interpret sections of the profile as stages of approaching the critical state of a forest ecosystem or meadow, tundra and boggy systems. The transitional belt between landscapes, ecotone, makes it possible to form a notion about the process of destruction of one system, which has not endured the pressure of changed conditions, and of development of another one.

The timber-line in mountains, if it is conditioned by climatic changes with height, but not by rock outcrops, avalanches, etc., is more suitable for fulfilling the task of studying critical states, than the timber-line on plain. In mountains limiting factors change at shorter distances. Besides a purely physical convenience for carying out research, it gives a certainty that in a limited interval other factors which should remain unchanged will not change, such as composition of mountain rocks, the impact of man and others.

In order to answer the question what determines the relative rate of the passing of an ecosystem through the critical state, we must choose landscape borders with different width of a transitional belt and try to find out on which factors this difference depends. To solve this task, the Institute of Geography of the USSR Academy of Sciences undertook field studies in the following two mountain regions: in the West Caucasus and in the East Sayan mountains, where the timber-lines possess necessary qualities. In both the regions, certains parts of a climatic timber-line were chosen for making profiles. Under these conditions, concrete reasons for the coming of critical states in forest ecosystems may be different: reduction of the growing period, decrease of the fertility of tree species, increase of the probability of a sun blight (Walter, 1968). However, for us it is important that any of these factors monotonously changes with altitude, which in such case may be accepted as a generalized index of an increase of the climate's bleakness.

A SHARP LIMIT OF THE FOREST, THE CAUCASUS

The first region where field studies were undertaken was the West Caucasus, within the territory of the Caucasian Biosphere Reserve. Here, on the southern slopes of the Chugush and Assara mountains with steepness of 25 to 35° we examined profiles in territories which had not been subject to economic use during several decades. The timber-line consisting of beech (Fagus orientalis Lipsky) with fir (Abies nordmanniana/Stev./Spach) was crossed by the profiles at the height of 1,880 m above sea level. Further up on the mountain of Assara there was a 50-metre transitional belt of filbert (Corylus avellana L.) with birch (Betula litwinowii A. Dol.) and maple (Acer trautwetteri Medw.). On the mountain of Chugush there turned out to be three transitional belts: a) of crooked beech up to 8 m tall with birch, b) of shrub forms of maple (Acer pseudoplatanus L.), birch and aspen (Populus tremula L.) with two species of ash (Sorbus caucasigena Kom. and S. subfusca/Led/Boiss.) and c) a belt of rhododendron (Rhododendron caucasicum L.). The total width of the three belts was 250 m. Still higher on both the profiles there was a belt of subalpine herbage. The change over from forest to transitional belts, as well as from the latter to meadow was extremely sharp (Figure 1). The border may often be marked by the edge of the canopy of marginal trees or by a clear edge of the contour of a bush massive. Near the upper limit, beech trees with straight trunks have 12 to 15 m in height, further down the slope it increases to 25 m and more.

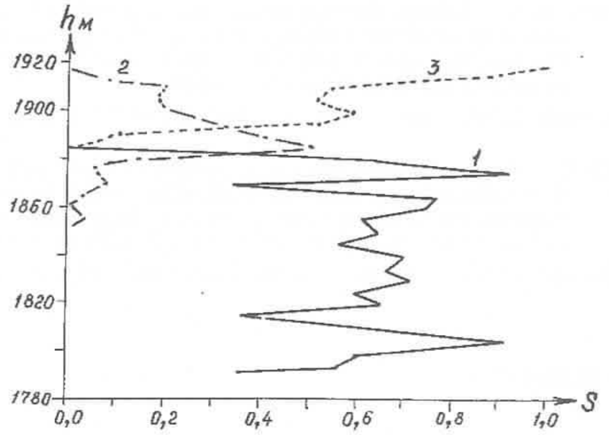


FIG. 1. — The change of the principal components of plant communities with height. Caucasus, profile on the mountain of Assara. 1 — beech, 2 — filbert, 3 — meadow grasses, 'h' — altitude above sea level, in m., 's' — projective coverage.

Moving from below to the timber-line, one may notice the features of approaching border only if he is very observant. Density of the canopy of the upper forest layer does not decrease, but in some places, on the contrary, it even increases, reaching 0,9. At the distance of 70 m from the timber-line, in the second layer, there appear some maple trees, and the area occupied by birch somewhat increases. In the bush layer there is an increase of the number of specimens of cherry laurel (Laurocerasus officinalis Roem.), rhododendron, honeysuckle (Lonicera caucasica Pall.) and a decrease of that of Caucasian bilberry (Vaccinium arctostaphylos L.). Probably species suffering from pressure under the canopy of beech and fir react especially strongly to an even very slight relaxation of the pressure for the part of dominant species. Within the meadow belt, it is still more difficult to notice the signs of the approach to the limit of landscapes (if one moves from the top downwards).

Geobotanical descriptions of grassy vegetation on plots of 10 by 10 m within the main and transitional belts have shown a complete absence of common species in the forest and the meadow belts and a mixed composition of grasses in the belts of crook-stem forest and bushes. All this testifies to a high degree of closure of meadow and forest cenoses. As relief and lithology of the loose cover are in both cases practically the same, while climatic differences at small drops in altitude are not great —the above peculiarities of the vegetation cover may be explained only by a strong transformation of the secondary phytogenic environment by forest and meadow cenoses. This assumption may be directly proved by sharp differences in light intensity under the forest canopy and in the open meadow, in the maximum wind force and depth of snow cover in both cases, in moistening and the structure of soil. Moutain-forest brown soils under the forest are characterised by the presence of litter of dead parts of plants. In the mountain-meadow soils, its place is occupied by a soddy horizon densely threaded by grass roots.

AN INDISTINCT LIMIT OF FOREST, THE EAST SAYAN MOUNTAINS

Field studies in the mountains of East Sayan were undertaken on the north-east slope of the Balakhtyn-Shele ridge. The profile crossed the timber-line at the height of about 1980 m. Larch taiga of Larix sibirica Ledeb. with undergrowth of birch (Betula rotundifolia Spach.) comes up to the timber-line from below. Above the timber-line there are associations of the belt of mountain tundras with predominance of Arctic-Alpine species: heathberry (Empetrum nigrum L.), dryad (Drias oxyodonta Juz.), bearberry (Arctous erythrocarpa Small). Strictly speaking, there is no border. Here it is replaced by a transitional belt within which the height of larch and the area occupied by it increase from the top downwards. In the upper part of the interval sparse trees 0,2 to 0,7 m high are spaced at great distances. Flag forms of crowns are quite common. At the distance of 150 m down the slope with steepness of 20° to 25°, the density of the stand reaches 0.7 and the height of trees — 8 m. (Figure 2). Further downwards the density and the height of the forest continue to increase. The grassy-undershrub cover represents a mosaic of patches, within which different species of plants predominate. In the upper part of the profile predominate associations of dryad, heathberry, bearberry, blueberry (Vaccinium uliginosum L.), in the middle part —the area of Cladonia sp.sp. somewhat increases, ruther down there begin predominating green moss species with Rhytidium rugosum/ Hedw./Kindb. and Aulacomnium turgidum Schwäegr. In the lower layer of vegetation the limit of high-altitude belts is outlined much sharper than in the arboreal one (see Figure 2), but outside the profile more gradual transitions are also met with. At the same time, geobotanical descriptions have shown that closure of certain associations is not great. In some pairs of associations up to 90 per cent of species are common.

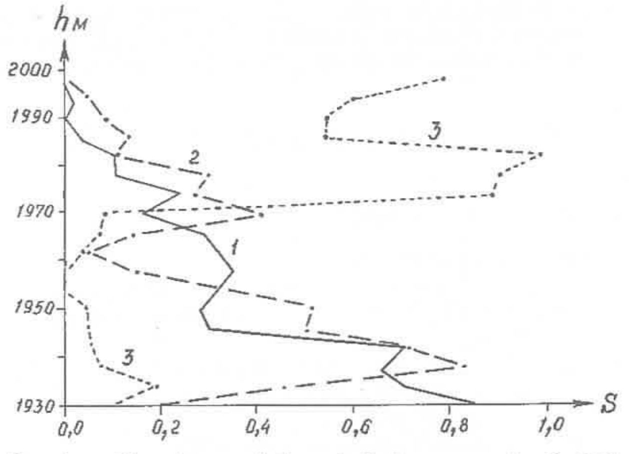


FIG. 2. — The change of the principal components of plant communities with height. The Sayan Mountains. 1 — larch, 2 — birch, 3 — heathberry, bearberry and dryad associations, 'h' — altitude above sea level, in m., 's' — projective coverage.

The indistinctness of the transition from the forest belt to the mountain-tundra one may be explained by the fact that larch transforms the phytogenic environment of plant communities in not so strong a degree as the plants of the Caucasus. Transparent crowns of larch retain little light in summer, while in winter needles fall off letting in frost and winds. The environment-forming role of moss, grasses and small shrubs is probably more significant. Soils of the forest and transitional belts differ little from the tundra ones: the former contains a soddy horizon up to 8 cm deep, while in the latter it reduces up to 2 cm.

DISCUSSION OF THE RESULTS

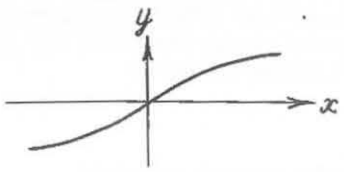
Let us compare distinct and indistinct limits of vegetation belts at the upper border of forest development. We may consider as an essential difference in the above examples different ability to transform phytogenic intercenotic environment by species-dominants of the Caucasus and the Sayan Mountains. In the first case dominants may be referred to strong edificators (transformers of the environment), in the second —to weak ones. It is proved both by direct observations of the soil environment, illumination within the cenosis and by indirect features of the secondary changes in the environment, first of all, indices of the closure of cenoses (indirect signs of the transformation of environment). The principal interactions on the border of forest and meadow are composed of positive links of vegetation with the environment transformed by it and negative links among ecosystems, as shown in the following scheme:

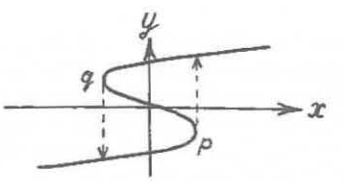
forest cenosis ↖ ↗ meadow cenosis
+ ↑ ↓ + ✕ + ↓ ↑ +
phytogenic environment phytogenic environment
of the forest of the meadow

So far as negative impacts on the competing plant community are produced in both directions by changing the inner environment, it is evident that with the increase of the degree of this change automatically increases suppression of plants —representatives of the competing community.

It may be supposed that the joint evolution of the principal species comprising the community has developed in them adaptability to "their own" secondary environment created by themselves. In other words, they transform the environment "for their own benefit". It is not difficult to imagine that such a system with strong edificators is able to survive even in those cases when macroclimate in a given area changes and becomes more corresponding to ecosystems of other types. The change of the inner environment by a phytocenosis turns out to be a means of maintaining the state of a homeostatic equilibrium of the system, "protection" against unfavourable influences. In the theory of catastrophs by R. Tom (Poston, Stewart, 1978) such situation is described by the model of a "fold" type. In the simplest form the analytical expression of the model looks as follows : $y^3 + ay = x$. In our case, variable 'x' may be interpreted as a limiting factor of the environment (macroclimate, 'y' —as one of the representative indices of the state of phytocenosis, for instance, the reserve of biomass,

'a' —coefficient, reflecting the force of interaction of the cenosis with the secondary environment, edificational ability of plants. When the values of 'a' are small, the diagram of the dependence of vegetation on climate looks like a straightened S-like curve.
With an increase of coefficient 'a' (intensification of the transformation of the secondary environment) the bend of the curve increases and a "fold" appears on it.





The model describes transition of ecosystems through a critical point both in time and in space. Let us suppose that we are in the subalpine belt and we decided to move towards the forest. Or, having armed outselves with patience we wait till the improvement of climate will make it possible for the limit of forest to come close to us. In both cases this will be expressed in the model by movement of the point along the lower branches of the curves to the right. In cenoses with weak inner links like the Sayan ones (the upper diagram) the transition to forest, represented by the upper branch of the curve, will be smooth. At every moment the state of the system will be controlled by climate, restructuring will have the character of a forced movement. A system with strong links, like in communities of the Caucasus (the lower diagram), after passing the critical point 'p' must survive the stage of a transitional process, which is not controlled by exterior conditions. As a result, a forest cenosis will form. This corresponds to the passing of the point over to the upper branch of the curve (dashed line). According to terminology of R. Tom, this transition has a character of a "catastroph".

If now, observing the events in time, we suppose that climate deteriorates, in the diagrams it will be represented by movement of the point to the left. Under the conditions of the Sayan mountains the replacement of forest by tundra will take place strictly in opposite sequence (the upper diagram), and in the Caucasus (the lower diagram) forest will retain its positions up to the moment 'q'. The section of the abscissa axis between projections of points 'p' and 'q' corresponds to climatic conditions in which, when there are strong inner links, both the meadow and the forest ecosystems are equally stable. This *"zone of hysteresis"* exists when there are analogous structures of feedback not only due to changes in time, but also in space, on one or on both sides from the real landscape limit. Evidently, within this zone in the Caucasian forests, glades cleared by cattle breeders have existed for hundreds of years. Within the Reserve, they show only a slight tendency toward overgrowing or they are not overgrown at all.

The "catastroph" model may probably also be applied to the limits in plains. It is known, that felling of forests near the borders with tundra or steppe often irreversibly transforms forest systems into tundra or steppe ones. Anthropogenic interference in these belts brings with itself an increased degree of risk.

CONCLUSION

With the use of the comparative-geographical method it becomes possible to show that a positive feedback of phytocenosis with phytogenic environment may serve as an essential mechanism of preservation of forest and meadow (or tundra) ecosystems near ecological limits of their existence. If the feedback is strong, the transition of ecosystems into ecosystems of other types takes place by the way of a sharp spatial border, similar to the timber-line in the Caucasus. The transitional process in time, as the space-time analogy makes it possible to conclude, should be completed relatively quickly. Otherwise, transformation goes on gradually, which is observed in the belt of replacement of forests by mountain tundra in the Sayan mountains. The space-time analogy makes it possible to assume that a similar gradual transition, when there are weak intersystem links, will also take place in time.

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List of Symbols

$\overset{+}{\rightarrow}$ — positive links;

$\overset{-}{\rightarrow}$ — negative links;
'y' — state of phytocenosis (reserve of biomass);
'x' — limiting factor of environment (macroclimate);
'a' — coefficient, force of interaction between the cenosis and the secondary environment;
'p', 'q' — critical points;
'h' — altitude above sea level, in m.;
's' — projective coverage.